XXVIII.—*The Affinities of* Palæocampa, *Meek and Worthen, as Evidence of the wide Diversity of Type in the earliest known Myriopods.* By Samuel H. Scudder*.

In an article on the structure of *Euphoberia* of the Mazon Creek nodules, published in this Journal a year ago †, the wide departure of modern myriopods from their ancient allies, in structure, general appearance, and habits, was clearly pointed out by detailed comparisons between the relics preserved in the Carboniferous rocks and the corresponding parts in modern types. A considerable number of specimens of Archipolypoda, as the ancient forms were termed, bearing out in every particular the points then brought forward, have since been examined, and have been fully represented in an illustrated memoir just published by the Boston Society of Natural History. Thanks to the local naturalists who have so well explored the beds of Mazon Creek, and who have furnished nearly all the material for the papers mentioned, I shall now attempt to show that *Palæocampa* is neither the caterpillar of a lepidopterous insect, nor a worm‡, but a myriopod of another new and strange type. Messrs. Carr and Bliss, of Morris, Ill., have sent me three specimens of *Palæocampa* in fine condition, better preserved and a little larger than the original, which has been lost by fire. Messrs. Meek and Worthen have also examined a second specimen; so that five in all have now been studied. Only one of these, that procured by Mr. Bliss, is preserved in such a way as to show the legs; and, until its discovery, the affinities of this animal would necessarily have remained very obscure.

But for my previous study of the Archipolypoda of Mazon Creek, and the revelation which these ancient types give of the divergence of structure between extinct and modern forms of Myriopoda, it would have been difficult to reach the full conviction that *Palæocampa* was a myriopod. It is a caterpillar-like segmented creature, 3 or 4 centim. long, composed of ten similar and equal segments besides a small head; each of the segments excepting the head bears a single pair of stout, clumsy, subfusiform, bluntly-pointed legs, as long as the width of the body, and apparently composed of several equal joints. Each segment also bears four cylindrical but

* Amer. Journ. Sci., Sept. 1882, pp. 161–170. Read before the National Academy of Sciences, in April 1882.

† Ann. & Mag. Nat. Hist. for June 1881, p. 437.

‡ *Cf.* Meek and Worthen, Proc. Acad. Nat. Sc. Philad. 1865, p. 52; *eosd.* Geol. Surv. Ill. vol. ii. p. 410, pl. xxxii. fig. 3, vol. iii. p. 565; Scudder, Geol. Mag. vol. v. p. 218.

spreading bunches of very densely packed, stiff, slender, bluntly tipped, rod-like spines, a little longer than the legs. The bunches are seated on mamillæ and arranged in dorso-pleural and lateral rows.

The individual rods have an intricate structure: instead of being striate, as supposed by Meek and Worthen in their last examination, they are furnished externally with about eighteen longitudinal equidistant ridges, about half as high as their distance apart; the edges of these ridges are broken into slight serrations at regular intervals about equal to the distance between neighbouring ridges, the highest point of each serration being towards the apex of the spine; the body of the ridge itself appears as if broken at each serration. The intervening space between neighbouring ridges is equally divided by two or three exactly similar but minute ridges, serrated at more frequent intervals. This serration of both larger and smaller ridges, with the apparent jointing or incision of the ridges to the base at the lowest point of each serration, gives the whole spine a jointed appearance; but a close inspection of the floor of the spine itself between the ridges shows no sign whatever of any break in its perfectly smooth surface. The diameter of the spines is only about one tenth of a millimetre; and yet it gives room for an exquisitely regular division of its periphery by seventy or more delicate ridges, every fourth one higher than the intervening, and all broken at minute intervals by uniform serrations. The preservation of these structures from Carboniferous times is only less remarkable than the occurrence, apparently so near the origin of the type to which it belongs, of ornamentation of such excessive delicacy, finish, complication, and regularity. I cannot discover that dermal appendages of such delicate and specialized organization occur anywhere today among arthropods, unless it be when developed as scales, as in Lepidoptera and occasionally in other groups of hexapods. Some chætopod worms have indeed hairs of curious asymmetrical structure, often very delicate and somewhat specialized, but never, so far as I can learn, to nearly so high a degree as here. The collection of these rods into fascicles is also not a little curious, and is again a feature known now in arthropods only in a few instances, such as some tufts of hairs in lepidopterous caterpillars like *Orgya*, or the pencils of hair-like scales in the males of some perfect Lepidoptera (*e. g.* at the tip of the abdomen in *Heliconia*, *Danais*, *Agrotis*, *Leucarctia*, &c.), or in the terminal fascicles of barbed hairs in the myriopodan genus *Polyxenus*.

There is no group of animals into which such a jointed

creature as this could fall excepting worms, myriopods, or the larvæ of hexapod insects. The certainty that this animal possessed a single pair of well-developed legs of identical character on every segment of the body behind the first segment or head is of itself sufficient evidence to exclude it both from the worms and from the larvæ of hexapod insects. No such legs or leg-like structures occur today in worms; and it would be idle to look for them in their ancestors of Carboniferous times. The only approach to such an appearance in hexapod larvæ is in the young of tenthredinous Hymenoptera, where, however, a difference of great morphological significance is found between the true or thoracic legs and the prolegs or those attached to the abdomen—a difference based on one of the most essential underlying features of their structure as hexapods. No such difference occurs in *Palæocampa*; and it is therefore impossible to conceive of it as the larva of a hexapod insect of any sort.

In myriopods only do we find a repetition of legs of exactly similar structure on every or nearly every segment of the body*; by this test *Palæocampa* is a myriopod; and now that we have found ancient types of this group, like the Archipolypoda, bearing huge and bristling spines arranged in series along the sides of the body, we need not be at all disconcerted at discovering this new type with longitudinal series of fascicles of stiff rods, although we cannot restrain our surprise and admiration at their exquisite intricate structure.

Accepting *Palæocampa* then as a myriopod, we may next ask what relation it bore to the myriopods of the same period and found in the same waters, and also to myriopods of today. The differences between the stout, forked, and bristling spines of the Archipolypoda and the close-set but spreading bunches of highly organized stiff rods of *Palæocampa* appear upon the barest statement. Were it not, however, for the complicated ornamentation of the rods themselves, the distinction between the fascicles of *Palæocampa* and the spines of *Euphoberia* would be hardly greater than that between the latter and the long hairs of an undescribed genus of Archipolypoda which has recently fallen under notice; so that to this feature alone we cannot grant so high an importance as to another which has already been named—the presence in *Palæocampa* of a single pair of legs (and consequently, to judge by analogy, of a single ventral plate) to each segment; while there are two ventral plates and pairs of legs to each

* Some smaller groups formerly, and by some authors still, considered as belonging to the myriopods must be excepted from this statement; their relation to *Palæocampa* will be discussed further on.

segment in Archipolypoda. This is a difference of profound significance, which has separated the prevailing types of myriopods down to the present day, lying as it does at the base of the distinctions between the living chilopods and diplopods. The discovery of this type is of the greater importance because we have hitherto known nothing of any chilopodiform myriopods previous to Tertiary times, unless Münster's dubious *Geophilus proavus* from the Jura possibly be an exception.

In studying the Archipolypoda we necessarily confine our comparisons with modern types to the Diplopoda, because of their common possession of the fundamental feature just named: in the same way the comparisons between *Palæocampa* and recent forms must be reduced to the common features or the radical distinctions which appear in studying the Chilopoda. Now, although the structure of *Palæocampa* may be far less perfectly known than that of the equally ancient *Euphoberia* and its allies, enough can be seen to point conclusively to wide and important differences between it and modern Chilopoda.

In Chilopoda, of which the modern *Scolopendra* or centipede is the type, the body is always depressed, formed of many segments, rarely as few as sixteen behind the head, each of which is compound, being formed of two subsegments, one of them atrophied and carrying no appendages; both dorsal and ventral plates are coriaceous, of nearly equal width, and possess no armature whatever excepting the simplest hairs, which are occasionally scattered over the surface. The larger subsegment bears a single pair of legs, which are composed of five slender, cylindrical, subequal joints beyond the coxa, and armed with a single apical claw; they are attached to the interscutal membrane uniting the distinct dorsal and ventral plates of each segment, and are therefore separated by the entire width of the broad ventral plates. The hindmost legs are transformed to anal stylets, while the first two pair are more profoundly transformed to subsidiary mouth-parts, the first becoming palpi and the second stout nippers. The head, really composed of eight primitive segments, is apparently made up of two, each of which is generally of about the same size as the body-segments and as distinctly separated; the stout biting-jaws, composed of the second pair of legs, spring from this second segment of the head, and the palpi or first pair of legs from the hinder part of the first cephalic segment; the anterior part of the same bears the many-jointed simple antennæ.

Passing now to the comparative study of *Palæocampa*, we

find that its body was, in all probability, cylindrical, composed of a limited number of segments behind the head, and the head itself, considerably smaller than the body-segments, is composed of only a single apparent segment. The legs of the segment immediately succeeding it are in every respect like those of the rest of the body, and have nothing whatever to do as auxiliary to the mouth. In this point alone we have a distinction as wide and incisive as any which separate the modern Diplopoda and Chilopoda. In the body-segments we discover no trace of any thing more than a simple ring without subdivision; but as the specimens indicate a coriaceous structure like that of modern Chilopoda, and no trace of the division between the dorsal and ventral plates can be seen in any of them, the separation of the segments into two subsegments, as in Chilopoda, one of them greatly atrophied, could hardly be apparent did it exist. But on the other hand, as we regard the second subsegment of Chilopoda as atrophied, we should expect to find it fully or partially developed in these creatures, which of all known ancient types are certainly the most closely related to them. Yet we find here no sign of any thing more than the simplest possible, uniform, leg-bearing segments, and of a very limited number. In one feature, however, they are not so simple as in Chilopoda; for, as stated, each is provided on each side with two pairs of mamillæ, supporting very large bunches of spreading rods, and the rods themselves sculptured in a very remarkable way. This distinction between the two types, though more striking and noticeable than any other, is in itself by no means so important as the others, but may be added to the catalogue; and it must have some weight, from the total absence of appendages of any sort (beyond scattered hairs) from the dorsal plates of Chilopoda. The position of these rows of fascicles and of the legs indicates that the ventral plates are only a little narrower than the dorsal, and probably of about the same extent as in the Archipolypoda; in this respect they do not differ to any important degree from modern Chilopoda. The legs were different in form; but their poor preservation in the only specimen in which they have been seen prevents any thing more than the mere statement of the following difference: while the legs of Chilopoda are invariably horny, slender, adapted to wide extension and rapid movement, those of *Palæocampa* are fleshy, or at best subcoriaceous, very stout and conical, certainly incapable of rapid movement, and serving rather as props.

These differences, which underlie every part of the body that is preserved in *Palæocampa*, show that while the general

accordance of grand features compels us to look upon *Palæocampa* as the precursor of the Chilopoda, we must separate it from them in the same way as we separate the Archipolypoda from the Diplopoda. For such a group the name of Protosyngnatha is proposed, indicating its ancestral relations to the chilopods, or Syngnatha, as they were called by Latreille.

There are, however, two aberrant groups of living animals more or less closely related to myriopods, and placed with them by some authors, with which also we shall compare *Palæocampa.* The first of these is *Peripatus*, our knowledge of which has been so much increased of late years, and especially by the researches of Moseley.

In external appearance *Peripatus* resembles an annelid, but is furnished with a pair of long jointed antennæ, and with numerous fleshy tapering legs, each armed at tip by a pair of claws; the legs, set wide apart, are obscurely jointed, the joints being perceptible only at the extreme tip and on the apical half of the inner side, above which are the large elongated openings into the nephridia. The entire body is of a leathery texture with no external sign of segments, or of the separation of the head from the rest of the body, except the appendages—namely the legs, the nephridia opening on the legs, and the ordinary appendages of the head. The same is true when the internal structure of the body is examined; for neither in the disposition of the muscles nor of the tracheal apparatus does it appear that one could judge whether a pair of legs represented one or more segments of the body; even in the nervous system it is only indicated by a small ganglionic swelling next each pair of legs. The tracheæ are like extended cutaneous glands, independent of one another, and scattered over the body; and the longitudinal muscles show no regular segmental breaks. This weakness of segmental divisions is nowhere paralleled among hexapods, arachnids, or myriopods, and is an indication of very low organization among arthropods generally. The number of legs indicates from fifteen to thirty-five segments in the body, according to the species. The first pair, as they are developed in the adult, are functionless as legs, and are situated (in the specimens I have examined—a South-American species, probably *P. Edwardsii*) midway between the antennæ and second pair of legs, and not only outside of, but at some distance from the mouth-parts, so that the latter are not furnished with auxiliary appendages borrowed from a segment behind the first, as in chilopods; this is further proven by the development of these parts in the two groups. The body is profusely covered above with corrugated papillæ, without regular distribution.

From this it will appear that *Palæocampa* differs in many essential features from *Peripatus*, and in most at least of these shows a higher organization. The segments are well separated from one another; and the head is distinctly marked. The number of segments is much less; and each bears clusters of appendages of a highly specialized character. Although no spiracles are present in the remains we have of *Palæocampa*, it is clear that respiration must have been effected through linearly disposed openings, since the muscular or mechanical requirements for the movement of a completely segmented body (especially if, as in *Palæocampa*, the segments bear a heavy armature) forbid the miscellaneous distribution of tracheæ, and demand a well-developed system with the same linear arrangement which we find in the armature. The best that can be said of the respiratory apparatus in *Peripatus* is that the tracheal bundles show a tendency toward "a concentration along two sides of the body, ventral and lateral." The possession, however, in each type, of a single pair of legs to every segment behind the head indicates an affinity which cannot be overlooked, and which is the more interesting since one of the types is very ancient and the other is universally looked upon as the existing survivor of an ancient type. The form of the body and of the fleshy legs is also similar; but there are minor points, and, however close the agreement between these forms, we cannot look upon *Palæocampa*, with its undoubtedly well-developed tracheal development, as in any sense the genetic predecessor of *Peripatus*; for the generally distributed tracheal apertures of the latter could not have developed from a serial disposition without a degradation of type, which, as Moseley points out, many other features combine with this to disprove. It may also be added that while the legs of *Palæocampa* are poorly preserved in the only specimen which gives a side view, the presence of nephridial openings, of such an extent and in such a place as in *Peripatus*, could hardly fail of detection, and they are entirely absent. The presence of these in *Peripatus* is one of the marks of its inferior organization, or rather of its alliance to an inferior type, the annelids.

The other aberrant group which we must specially notice is *Scolopendrella*, placed at first among Chilopoda, but recently shown by Ryder and Packard to differ from them in very important features, in some at least of which it agrees with *Palæocampa*. The researches of these naturalists, as well as the earlier observations of Menge, clearly prove that it must be separated from the myriopods altogether, and that it is certainly provided with many points of affinity to the Thy-

sanura. Ryder suggests for it an independent place between the Myriopoda and Thysanura, under the name Symphyla. Packard, with better reason, would place it within the Thysanura, under which head he would also include the Collembola and Thysanura proper, or Cinura, as he terms them.

Scolopendrella, as these authors point out, differs from the Chilopoda in that the appendages of the segment behind that furnishing the mouth-parts proper do not serve as auxiliary organs for manducation, but are developed, like those of the succeeding segments, as legs, while the mouth-parts resemble those of Thysanura, and differ from those of Chilopoda: indeed the whole head is decidedly thysanuriform, the legs are provided with a pair of claws, and the terminal segment bears a pair of caudal stylets with a special function. Besides these points, the possession of a collophore is distinctively thysanuran; and the position of the stigmata, between the legs, is different from the position they uniformly maintain in Chilopoda, while it only adds to the great irregularity of place seen in Thysanura. On the other hand, the identity of form in the thoracic and abdominal segments, the full development, upon the abdominal segments, of jointed legs like those of the thoracic segments, and the occasional alternation of leg-bearing and apodal segments in the abdomen, are striking marks of its real affinity to the chilopods. Abdominal appendages, homologous with legs, but unjointed, do, however, occur in Thysanura to a greater degree than in other hexapods, so that we can hardly refuse to admit these polypodous creatures as lowest members of the subclass of insects proper, although they are the only non-hexapodal type.

Now the separation of the head and its appendages from those of the next succeeding segment distinguishes *Palæocampa* from the Chilopods in the same way as it does *Scolopendrella*; so, too, the segments behind the head in *Palæocampa* and *Scolopendrella*, alone of all arthropods in which the head is thus clearly separated, agree in showing no distinction whatever between what may be looked upon as thoracic and what as abdominal, whether in the form of the segment itself or in the appendages of the segments. These are certainly fundamental points; but when we have mentioned them we have reached the end of all possible affinities or points of resemblance, unless we may consider the minute structure of the rods in the fascicles of *Palæocampa* paralleled by the well-known delicacy of organization of the scales in other Thysanura, though they do not exist in *Scolopendrella*. The limited number of abdominal segments might be looked upon as a further point, were it not that the number is even less than

in *Scolopendrella* or in the Cinura, and that the Pauropida among diplopod myriopods have in some instances even a still smaller number. On the other hand, the character of the legs, the apparent absence of a double claw at their tip, the peculiar armature of the fascicled rods, which form so striking a feature in *Palæocampa*, the want of any caudal stylets, and the complete uniformity of the segments of the body unprovided with distinct dorsal scutes distinguish *Palæocampa* not only from *Scolopendrella*, but from all Thysanura whatever; the general form of the body, too, is altogether different from any thing occurring there, even its cylindricity being foreign to the Thysanura, excepting in their highest types among the Collembola. It seems therefore clear that the points of affinity between *Palæocampa* and *Scolopendrella*, with the single exception of the separation of the head and its appendages from the body, are precisely those in which *Scolopendrella* is chilopodan, and that the assemblage of features which our fossil presents are therefore chilopodan rather than thysanuran.

Regarding *Palæocampa*, then, as a myriopod, though of a type very distinct from any known, whether living or fossil, we are brought face to face with two remarkable and somewhat parallel facts:—First, that *in this ancient myriopod*, as old as any with which we are acquainted, carrying us back indeed as far as any traces of wingless tracheate arthropods have been found, and therefore presumably not far from the origin of this form of life upon the earth, *we find dermal appendages of an extraordinarily high organization*, more complicated, as we have pointed out, than any thing of the sort found in living arthropods, excepting the more varied but not more exquisite scales of several orders of hexapods—a form of appendage which it would seem, on any genetic theory of development, must have required a vast time to produce, but which we now seem to find at the very threshold of the apparition of this type of arthropod life.

Second, that *at this early period*, in marked contrast to what we find in other groups of articulated animals, *the divergences of structure among myriopods was as great as it is today*. This is the more surprising because we possess only imperfect remains of a few types; and yet from what we already know of the Archipolypoda, on the one hand, and of the Protosyngnatha on the other, they are found to differ quite as much as the Diplopoda and Chilopoda, and in points fully as important as those which separate so sharply these great modern groups. Whether they are to be looked upon, one as the ancestor of one, the other of the other, of these modern groups, is another

question. It would certainly be reasonable to consider the Archipolypoda as the common ancestors of both the Chilopoda and Diplopoda—and possibly the Protosyngnatha as the descendants on one line of a primitive type which, on another line, has retained its integrity up to the present day in *Peripatus* (and on possibly a third line has reached *Scolopendrella*), while on that which produced *Palæocampa* it has not, so far as we know, survived the Carboniferous epoch. With the facts of structure of ancient and modern types now before us, we are compelled, on any genetic theory, either to presume a great acceleration of development in earlier times or to look for the first appearance of myriopods at a vastly remoter epoch than we have any reason to do from the slighter hints in the rocks themselves—a period so remote as to antedate that of winged insects, which are now known from rocks older than any which have yielded remains of myriopods. In a memoir on Devonian insects, the concluding portion of which was republished in this Journal *, I showed the probability, on developmental grounds, that some of the Carboniferous insects, "together with most of those of the Devonian, descended from a common stock in the Lower Devonian or Silurian period, and that the union of these with the Palæodictyoptera (of the Carboniferous) was even further removed from us in time." The structural relations of myriopods and hexapods render it probable that the former preceded the latter; and in complete accordance with this expectation, the structural relations of the oldest fossil myriopods indicate their apparition at a period earlier than that to which the winged insects are hypothetically assigned. This would compel us to consider the earlier type as aquatic, for which we have presumptive evidence in the structure of the Euphoberidæ, and renders it all the more surprising that the penetrating researches of the last thirty-seven years, since the first Carboniferous myriopod was discovered, have not yielded the slightest trace of fossil myriopods below the Coal-measures. This discrepancy between fact and hypothesis should never be lost sight of, and should stimulate to more searching investigations, particularly of those articulates of the older rocks whose affinities have not been satisfactorily settled.

* Am. Journ. Sci. vol. xxi. p. 117.